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INHERITANCE OF FECUNDITY IN THE DOMESTIC FOWL¹

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THERE are under discussion at the present time two general views regarding certain fundamental points in heredity. Each of these points of view has its zealous adherents. On the one hand, is what may be designated the "statistical" concept of inheritance, and on the other hand, the concept of genotypes. By the "statistical" concept of inheritance is meant that point of view which assumes, either by direct assertion or by implication, that all variations are of equal hereditary significance and consequently may be treated *statistically* as a homogeneous mass, provided only that they conform to purely statistical canons of homogeneity. This assumption of equal hereditary significance for all variations is tacitly made in deducing the law of ancestral inheritance, when individuals are lumped together in a gross correlation table.² The genotype concept, on the other hand, takes as a fundamental postulate, firmly grounded on the basis of breeding experience, that two

¹ Papers from the Biological Laboratory of the Maine Experiment Station, No. 25. This paper was read at the meeting of the American Society of Naturalists at Ithaca, December, 1910.

² For a more detailed discussion of this point see a paper by the present writer entitled "Biometric Ideas and Methods in Biology: their Significance and Limitations," in the *Revista di Scienza* (in press).

sorts of variations can be distinguished, namely those (*a*) that are represented in the germinal material and are inherited without substantial modification, as in "pure lines," and those (*b*) that are somatic and are not inherited. By anything short of the actual breeding test it is quite impossible to tell whether a particular variation observed in the soma belongs to the one category or to the other. As I have tried to emphasize in other places, it is both to be expected on this view of inheritance, and is also the case in actual fact, that the somatic manifestation or condition of any character is a most uncertain and unreliable criterion of the behavior of that character in breeding. Finally under the genotype concept, of course, the whole array of facts brought out by Mendelian experiments find their place.

Now while certain adumbrations of the genotype concept have long been current in biological speculations in regard to heredity, this general view-point owes its grounding in solid facts primarily to Johannsen's work with beans and with barley. It is to be noted that in these cases, as well as in most of the investigations of the pure line theory which have followed Johannsen's work, the organisms used have been such as reproduced either by self-fertilization, or by fission, or by some vegetative process. This brings us to the consideration of a question of great importance, both theoretical and practical. In cases of dioecious organisms, where a "pure" pedigree line in the sense that such lines are found in beans or in *Paramecium* by definition can not exist, has the genotype concept any bearing or significance? In a general way it obviously has. Probably no one (except possibly some of the ultra-statistical school) could be found who would deny that in general a distinction is to be made between variations having a gametic and those having merely a somatic basis. But specifically how far has the genotype concept any application in case of "non-selfed" organisms? Johannsen in his "Elemente" has thoroughly analyzed Galton's material and

shown that it is capable of a satisfactory and reasonable interpretation on the genotype hypothesis, and East and Shull have gone far in the analysis of genotypes in maize. This, however, is only a beginning. There is the greatest need for careful, thorough investigations of the inheritance of characters showing marked fluctuating variation in organisms having the sexes separate. Here lies one of the crucial fields in the study of inheritance to-day. Through the brilliant results in Mendelian directions and from the study of really "*pure*" lines we are getting clear-cut ideas as to the inheritance of qualitatively differentiated characters, such as color, pattern and the like, on the one hand, and in regard to the inheritance of quantitative variation in self-fertilized or non-sexually reproducing organisms, on the other hand. But beyond all these lie the difficult cases where in dioecious forms quantitative variations must be dealt with. If these can be cleared up and brought harmoniously into a general scheme or view-point regarding inheritance, we shall have gone a long way in the solution of this world-old biological problem.

For some four years past the writer has been engaged in a study of the inheritance of fecundity in the domestic fowl. The problem presented here is an important one from the practical as well as the theoretical standpoint. If definite and sure methods of improving the average egg production of poultry by breeding can be discovered it will mean much to the farmers of the nation. At the same time egg production is a character in some ways well adapted to furnish definite and crucial data regarding inheritance. Variations in egg production are readily measured, and can be directly expressed in figures.

The general results of this study of the inheritance of fecundity may be said, in a word, to be, so far as they go, in entire accord with the genotype concept, and not to agree at all with the "*statistico-ancestral*" theory of inheritance. Indeed, so ill is the accord here that the chief exponent of the latter doctrine has recently attempted to

throw the whole case out of court³ by asserting that fecundity is not inherited in fowls, and that the present writer's investigations show essentially nothing more than that. It will be the purpose of this paper to present some figures sufficient to indicate with some degree of probability, I think, first that egg production in fowls is inherited, and second that it is probably inherited in accord with the genotype concept, in spite of the fact that we do not and can not here have "pure lines" in the strict sense of Johannsen's definition. In the present paper, owing to limitations of space, the whole of the data in hand obviously can not be presented. Only a few illustrative cases can be given here.

Before entering upon the discussion of the evidence it is necessary to call attention to two points. The first is in regard to the unit of measuring egg production used in the work. For reasons which have been discussed in detail elsewhere⁴ the unit of study has been taken as the egg production of the bird before March 1 of her pullet year. This "winter production" is a better unit for the study of the inheritance of fecundity than any other which can be used practically. All records of production given in this paper are then to be understood as "winter" records, comprising all eggs laid up to March 1 of the first year of a bird's life. It may be said that the "normal" mean winter production of Barred Plymouth Rocks (the breed used in this work) is fairly indicated by the 8-year average of the Maine Station flock. This average November 1 to March 1 production is 36.12 eggs.⁵ This figure is based on eight years continuous trap-nesting of the flock with which the present

³ Pearson, K., "Darwinism, Biometry and some Recent Biology, I," *Biometrika*, Vol. 7, pp. 368-385, 1910.

⁴ Bull. Me. Agr. Exp. Sta., No. 165. U. S. Dept. Agr. Bur. Anim. Ind., Bul. 110, Part II.

⁵ It should be said that up to and including the winter of 1907 only the November 1 to March 1 records are available as a "winter" record. Since that time the small number of eggs laid before November 1 (on the average two or three per bird) are included in the "winter" totals. These, then, give, as stated, the total production up to March 1.

work was done, carried out before these investigations were begun.

In the second place it is desirable to call attention to some of the difficulties which attend an attempt to analyze the inheritance of the character egg production. The most important of these is the fact that this character is not visibly or somatically expressed in the male. A male bird may carry the genes of high fecundity, but the only way to tell whether or not this is so is to breed and rear daughters from him. All Mendelian workers will agree that it is sometimes difficult enough to unravel gametic complexities in the case of characters expressed somatically. It is vastly more difficult when only one sex visibly bears the character. In the second place a very considerable practical difficulty arises from the fact that egg production is influenced markedly by a whole series of environmental circumstances. The greatest of care is always necessary, if one is to get reliable results, to insure that all birds shall be kept under uniform and good conditions. Further, on this account, it is necessary to deal with relatively large numbers of birds. Some of the important conditions to be observed in work on fecundity have been discussed elsewhere⁶ and need not be repeated here.

Turning now to the results we may consider first

THE EFFECT OF SELECTION FOR FECUNDITY IN THE GENERAL POPULATION

On the "statistico-ancestral" view of inheritance it would be expected that if fecundity were inherited at all this character would respond to continued selection. That is, it would be expected, if the highest layers only were bred from in each generation, that the general flock average would steadily, if perhaps slowly, increase and that any level reached would be at least maintained by continued selection. In 1898 an experiment in selecting for high egg production was begun at the Maine sta-

⁶ Me. Agr. Exp. Sta. Ann. Rept. for 1910, p. 100.

tion. In this experiment only such females were used as breeders as had laid over 150 eggs in their pullet year (corresponding roughly to an average winter production of 45 or more eggs) and the only males used were such as were out of birds laying 200 or more eggs in the year. This experiment was continued until the end of 1908. The selection, be it understood, was based on the egg record alone, and no account was kept of pedigrees or of genotypes. Every female with a record higher than 150 eggs in the year was used as a breeder regardless of whether her high fecundity was genotypic or phenotypic.

The results of this selection experiment covering a period of nine years have been fully reported elsewhere.⁷ Here it needs only to be said that the net outcome of the experiment was to show that there was no *steady* or *fixed* improvement in average flock production after the long period of selection. There was no *permanently* cumulative effect of the eight (in the last year) generations of selected ancestry. So far from there having been an increase there was actually a decline in mean egg production concurrent with the selection, taking the period as a whole. During parts of the selection period, however, as for example the years 1899–1900 to 1901–02, inclusive, and the years 1902–03 to 1905–06, inclusive, an improvement from year to year was to be noted, but in each case the flock dropped back in intervening years. This is an important point, the meaning of which is now clear. The flock average from year to year depended largely upon *whether the breeders of the year before had had their high fecundity genetically represented or only somatically*. In some years the selection was fortunate in getting nearly all the breeders from good (*i. e.*, “high production”) genotypes or from good *combinations* of genes. In other years just the opposite thing happened: the high layers chosen as breeders came from low geno-

⁷ U. S. Dept. Agr. Bur. Anim. Ind., Bul. 110, Parts I and II, 1909 and 1911. *Zeitschr. f. indukt. Abst. u. Vererb.-Lehre*, Bd. 2, 1909, pp. 257–275.

types or combinations of genes. The general upshot was that while the selection of *high layers* merely as such was systematic year after year the result attained in the general flock production was entirely haphazard and uncertain. This is exactly what would be expected on the genotype hypothesis, but not on the "statistico-ancestral."

TABLE I

MEAN WINTER (NOVEMBER 1 TO MARCH 1) EGG PRODUCTION DURING THE SELECTION EXPERIMENT

Year	Mean Winter Production
1899-1900	41.03
1900-01	37.88
1901-02	45.23
1902-03	26.01
1903-04	26.55
1904-05	35.04
1905-06	40.66
1906-07	21.44
1907-08	15.92

The actual course of the average winter egg production (not hitherto published) during the period is given by the figures of Table I and shown graphically in Fig. 1.

Certainly the first line of evidence, derived from a long-continued experiment, involving more than 2,000 individuals, gives no support to the "statistico-ances-

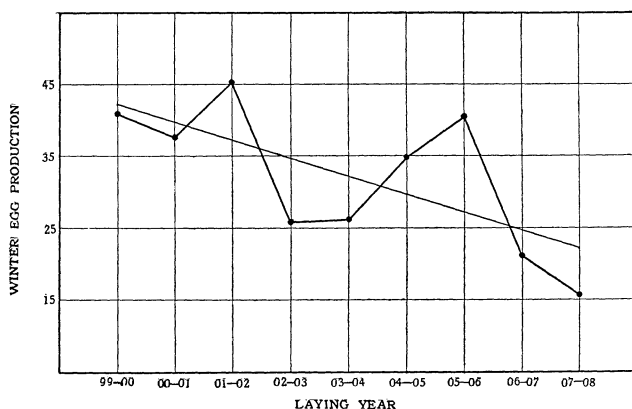


FIG. 1. Diagram showing the course of average winter egg production during the period covered by the mass selection experiment.

tral" theory and indeed is in flat contradiction to one of the most fundamental tenets of that faith.

Let us next consider the question,

ARE SOMATICALLY EQUAL VARIATIONS IN FECUNDITY OF
EQUAL HEREDITARY SIGNIFICANCE?

In the spring and summer of 1907 were reared 250 pullets, all of which were the daughters of hens that had laid approximately 200 or more eggs in the first year of their life. This group of mothers was reasonably homogeneous in respect to records of egg production. All had laid about the same number of eggs. Their daughters were, however, far from a homogeneous lot with respect to egg production.⁸ It is plain from the results obtained in that experiment that the egg record of a hen is a most unreliable criterion of the probable number of eggs which her daughters will lay. This is demonstrated by examination of individual cases. Thus consider the two mothers nos. 253 and 14. Their winter production records were nearly identical (65 and 66 eggs, respectively). Their daughters' average winter productions were 23.87 and 2.40 eggs, respectively! Certainly it seems reasonable to conclude that the gametic constitutions involved in the breeding of 253 and 14 were quite different, though both these hens laid the same number of eggs. Again, take birds no. 386 and 911. One had a winter record of 55 and the other of 52 eggs. Yet their daughters' average winter productions were, respectively, 4.88 and 27.33 eggs. Many more instances of this kind could be brought forward. Taken together, the whole evidence shows beyond the shadow of a doubt that the presence of high fecundity in an individual, and that factor which makes high fecundity appear in the progeny, are two very different things, either of which may be present in an individual without the other. We plainly have here the basis for the distinction of phænotypes and genotypes just as in beans.

⁸ Full details regarding this experiment have been published as Bull. 166, Me. Agr. Exp. Sta., 1909. See particularly Table I.

THE INHERITANCE OF EGG PRODUCTION IN PEDIGREE LINES

Let us now consider some of the evidence that such things as genotypes of fecundity really exist in fowls. We may first examine some representative pedigrees covering four generations and showing the occurrence of high and low fecundity lines.

As a typical example of a high fecundity pedigree line in which the high fecundity is genotypic, line D5D39 may be considered. In the presentation of this and other pedigree tables the following conventions are adopted. The band numbers of the birds are in bold-faced type, and following the band number of each female, her winter egg record is given in italic figures enclosed in parenthesis. The band numbers of males are given in italics.

PEDIGREE LINE D5D39

♀ D39 (62) × ♂ <i>D5</i>	{	♀ E232 (69) × ♂ <i>555-0</i>	{	♀ G 10 (100)	
				14 (99)	
				88 (23)	
				524 (16)	
		{		♀ G 12 (16)	
				19 (70)	
				39 (100)	
				53 (44)	
		{		81 (34)	
				85 (73)	
				192 (57)	
				213 (29)	
	{	237 (55) × ♂ <i>554</i> <i>Mean</i> = 62	{	♀ G 18 (61)	
				27 (83)	
				46 (116)	
				196 (56)	
	{	♀ 347 (69) × ♂ <i>562</i>		211 (36)	
				248 (67)	
		{		♀ G 11 (47)	
				134 (111)	
				165 (35)	
				198 (39)	
		{		506 (16)	
				<i>Mean</i> = 57.74	

This line is shown graphically in Fig. 2.

Little comment on this pedigree line is necessary. We see a certain high degree of fecundity faithfully reproduced generation after generation. Different males were

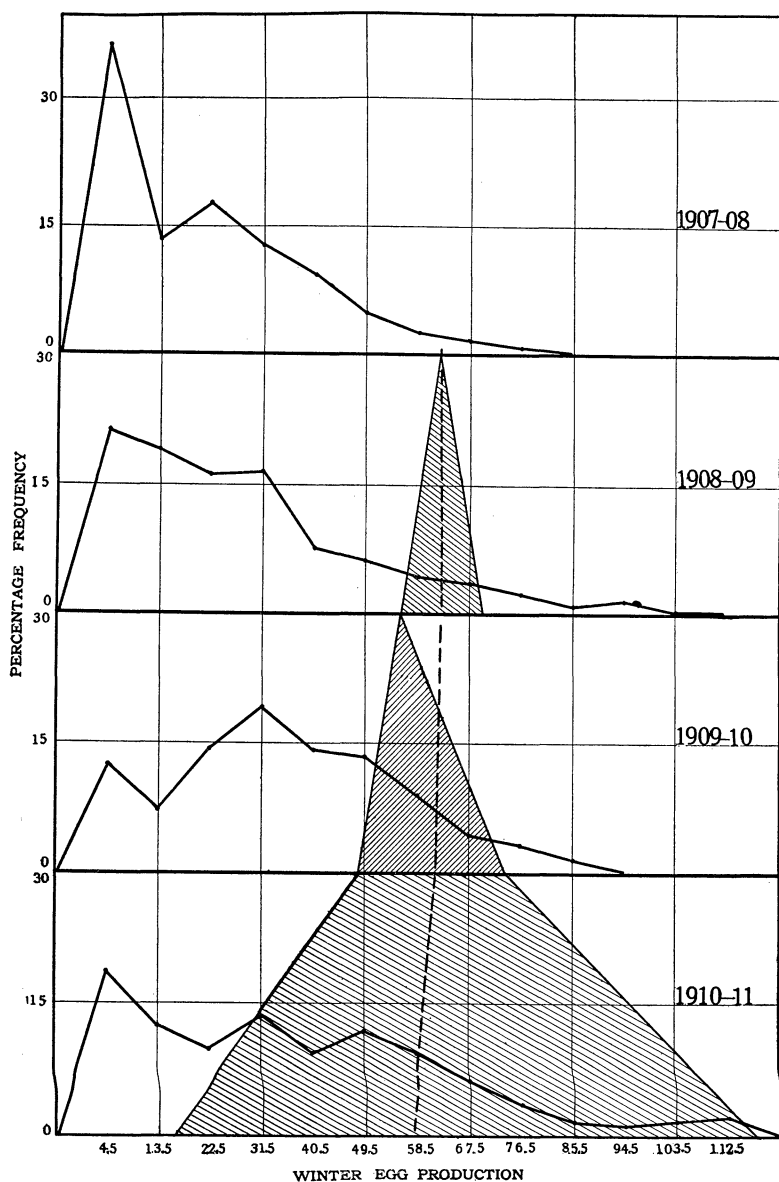


FIG. 2. Diagram showing range of variation and mean fecundity in each generation of line D5D39. The main polygons of variation give the distribution of fecundity in the general flock in each generation. The cross-hatched areas represent the pedigree line, and the heavy dotted lines through these areas represent the mean fecundity of the line in each generation.

used with different females, but in every case the males used were from high fecundity lines and were believed to carry this quality in their germ cells either in homozygote or heterozygote condition.

In marked contrast to the last example let us consider the *low* fecundity line D61D168. It is a troublesome matter to propagate the low fecundity lines, because of the difficulty of getting a sufficient number of eggs during the early part of the breeding season. The line D61D168 is of interest not alone as an illustration of a typical low line, but also because there appeared in it a mutation, or something very like one. We will consider here only the main line and not the mutant.

PEDIGREE LINE D61D168

♀ D168(33) × ♂ D61	♀ E231(25) × ♂ 552	♀ F233(32) × ♂ 573-0	{	♀ G221(16)
	419(9) × ♂ 551	♀ F165(7) × ♂ 569		430(12)
	209(38) × ♂ 555-0			477(1)
	313(26) × ♂ 554	{		Mean=9.67
	363(11) × ♂ 550			♀ F250(20)
				174(21)
		♀ F249(30)		
		Mean=22		
		15(18)		
		163(9)		
	200(12)			
	141(0)			
	116(28)			
	151(11)			
	24(23)			
	Mean=17.5			
	♀ F248(48) ⁹			

This line is shown graphically in Fig. 4, in which the mutant and its progeny are also shown.

A low line in which no mutant has appeared, but in which also the mean production is not so low as in line D61D168 is D65D366. Since the egg production has not been so low in the early part of the breeding season with this line it has been easier to propagate it.

⁹ This was the mutant referred to. Its progeny will be considered later. See p. 335.

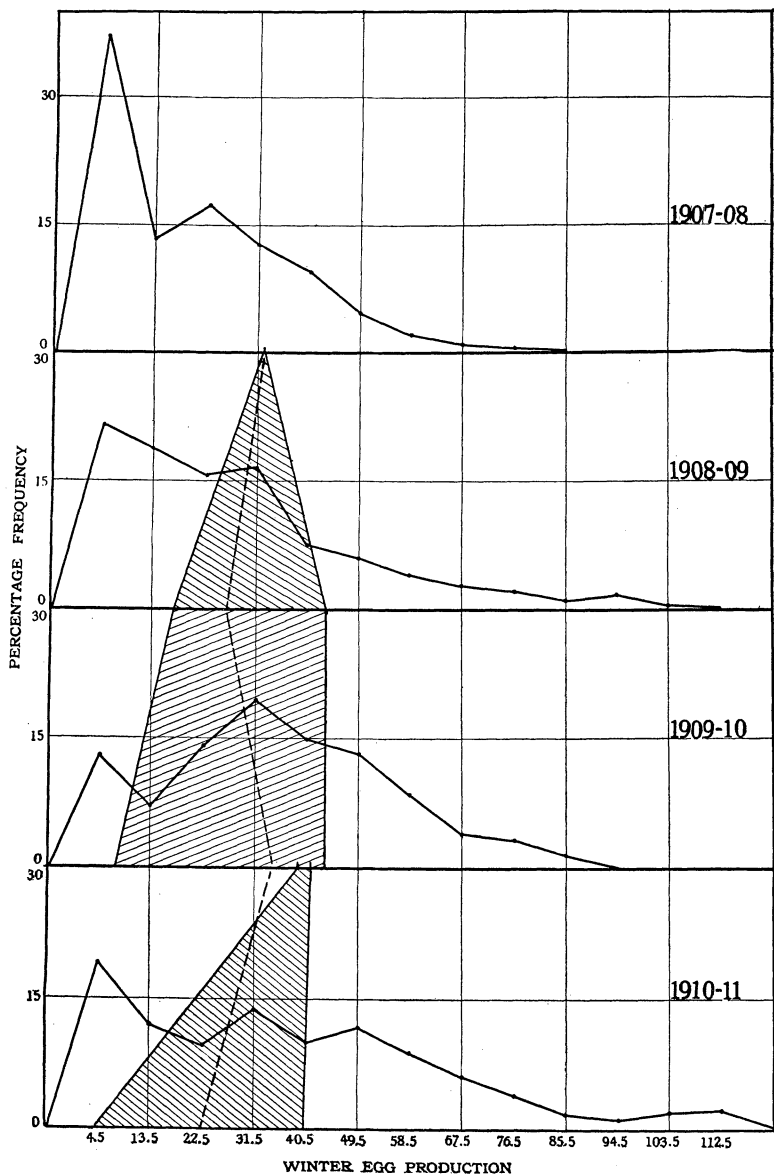


FIG. 3. Diagram showing range of variation and mean fecundity in each generation of line D65D366. Significance of lines and cross hatching as in Fig. 2, *q.v.*

PEDIGREE LINE D65D366

♀ D366(33) × ♂ D65	♀ E239(24) × ♂ 553	{ <div> ♀ F309 (OD)¹⁰ 263(44) 362(43) 216(41) × ♂ 569 </div> }	{ <div> ♀ G 34 (4) 42 (37) 56 (40) 164 (5) </div> }
	224(43) × ♂ 554	{ <div> ♀ F301 (7) 223(14) 221(42) </div> }	
	354(15) × ♂ 551	{ <div> ♀ F242(21) 221(39) × ♂ 566 </div> }	{ <div> ♀ G 65 (28) 209 (33) 267 (25) 502 (21) 544 (8) </div> }
	331(31) × ♂ 552-0		
	344(17) {	{ <div> × ♂ 550 × ♂ 528 </div> }	{ <div> ♀ F271(37) ♀ F171(46) </div> }
	Mean=26	Mean=33.4	Mean=22.33

This line is shown graphically in Fig. 3.

In the examples thus far given we have had to do with pedigree lines in which a given degree of fecundity reappeared from generation to generation with practically no change. In two instances quite certainly, and possibly in several others, a new and distinct variation has suddenly appeared within a line and thereafter bred true, thus presenting the characteristic phenomena of mutation. The most striking instance of this sort occurred in line D61D168 and may be given here in detail. The main part of this line has already been discussed (p. 331). It will be recalled that it is a line of low fecundity. In 1908 there appeared in it one individual of distinctly higher fecundity than any other bird in the large family of that year. This individual when bred produced only high layers. In the next generation two of these daughters were bred to males known to belong to high fecundity genotypes (♂♂ 554 and 566). One of these matings unfortunately produced no adult female offspring. The other led to the production of six adult daughters, all of which are relatively high layers, with the single exception of G495, which has a record of only one egg, and that record is doubtful. This bird has probably never laid an egg, and almost certainly is pathological.

¹⁰ Bird died during winter period.

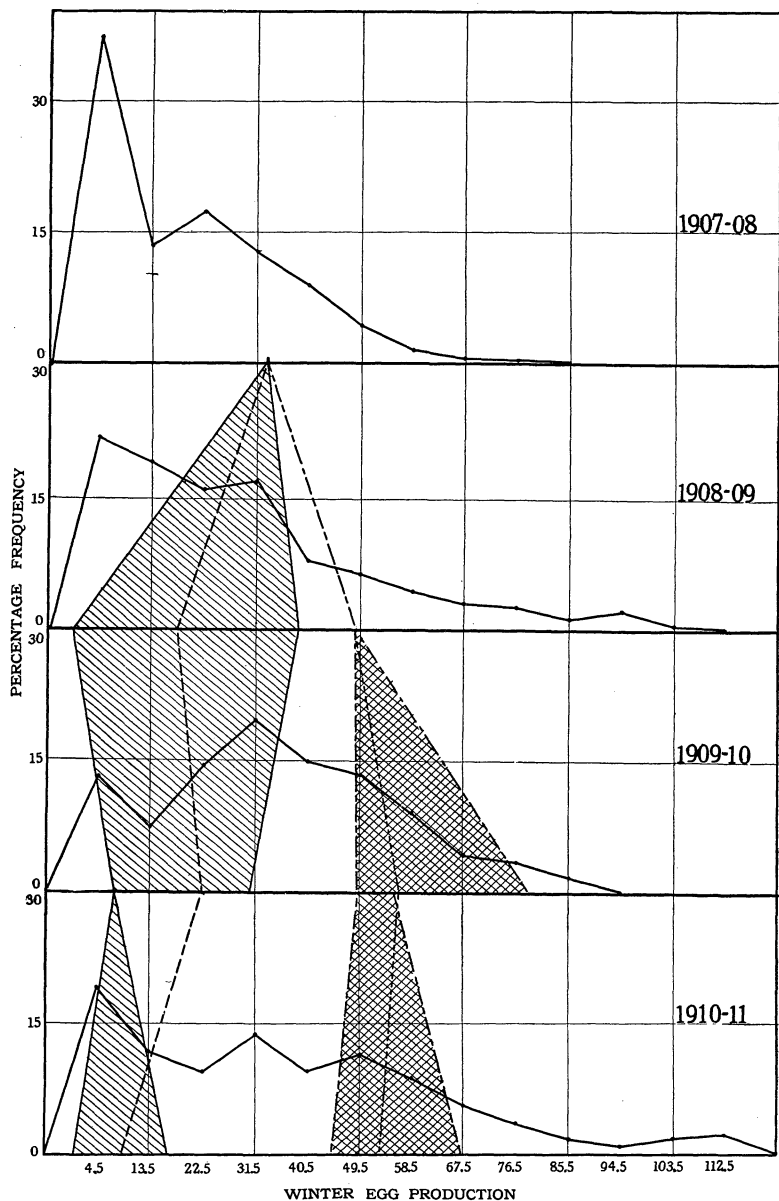


FIG. 4. Diagram of pedigree line D61D168. The significance of lines is the same as in Figs. 2 and 3, except that the mutant line is double cross hatched. For the sake of simplicity E495 and the daughters of D31 are omitted in the 1910-11 generation.

Leaving this bird out of account because pathological, the mean winter production of the family is 52.8 eggs, very strikingly different from the average (9.67 eggs) of the birds of the same generation in the main low line in which the mutation appeared.

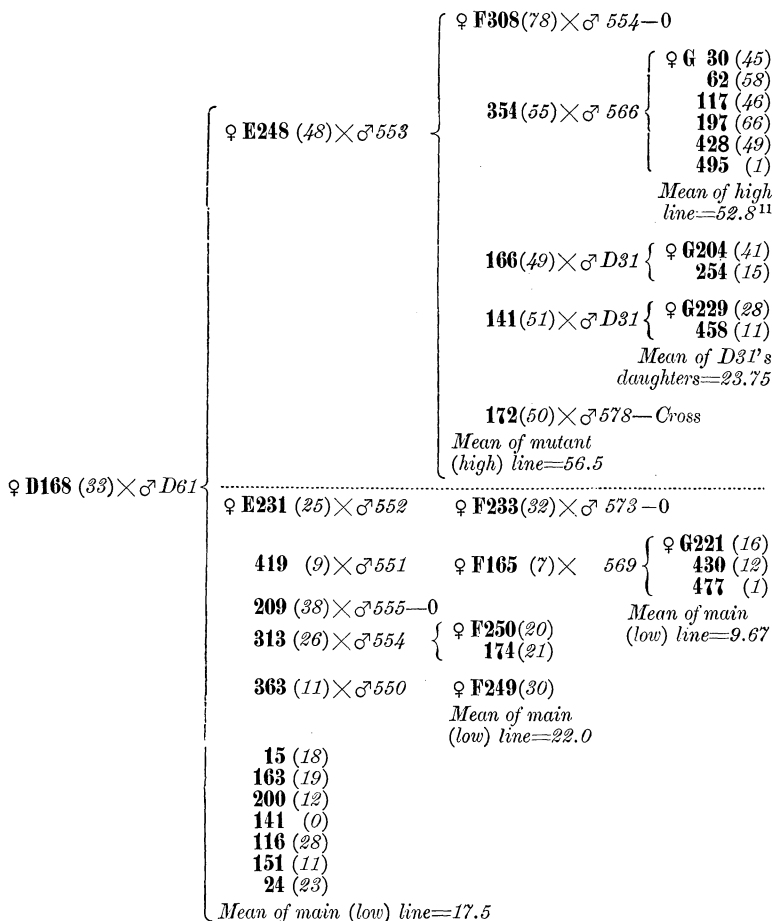
Two other daughters of the mutant E248 were mated to ♂D31, a bird known not only to belong to a genotype of mediocre to low fecundity, but to be remarkably prepotent in respect to this character, so that practically regardless of the females with which he has been mated the get has been uniformly poor in respect to egg production. Four adult females resulted from the two matings under discussion. They have an average winter production of 23.75 eggs. There are several possible explanations of this result, but the most probable is that we have here simply one more instance of the extraordinary prepotency of ♂D31.

The last of the daughters of the mutant was mated to a cross-bred male, no. 578, and consequently the progeny can not fairly be compared with the pure Barred Rocks in respect to fecundity.

The facts here briefly discussed are shown in the following table and graphically in Fig. 4.

It is apparent from the table and the diagram that the main line and the "mutant" line are entirely distinct. Indeed they do not overlap in their ranges even excepting only the pathological individual G495. The "mutant" pullet E248, for some reason or other, possessed the capacity both to lay a relatively large number of eggs, and the genes necessary to make this quality appear in her progeny. Whether this individual is to be regarded as a true "mutation" would appear to be largely a question of definition. In the writer's opinion the most probable explanation is that E248 is a Mendelian segregation product. That is, let it be supposed that both D168 and D61 were heterozygous with respect to degree of fecundity, and were producing in some (unknown) ratio both "high fecundity" and "low fecun-

PEDIGREE LINE D61D168 (COMPLETE)



dity" gametes. Then E248 may be supposed to have originated from the union either of two "high fecundity" gametes or one high and one low fecundity gamete. She then would be either a DD or a DR bird, on the assumption, which the facts seem to support, and which I have more fully discussed elsewhere,¹² that high fecundity is dominant over low.

¹¹ Omitting G495. See text.

¹² "Inheritance in 'Blood Lines' in Breeding Animals for Performance, with Special Reference to the '200-egg' Hen," Rept. Amer. Breeders' Assoc., Vol. VI, 1911 (in press).

The subsequent breeding history of E248 indicates that it was probably a DD bird, though the reasons for this opinion can not be fully gone into here. The general view, recently emphasized by Nilsson-Ehle,¹³ that phenomena of mutation are, in many cases at least, merely cases of Mendelian segregation has much evidence in its favor.

The pedigrees which have been given are merely illustrations. Many other similar ones might be cited from the records in hand did space permit. In the experiments during the past three years the attempt has been made to propagate separately lines of high, medium and low fecundity. In the course of this work it has been found that lines of high fecundity were nearly if not quite as likely to have originated with individuals of a low record of production as with those of a high record. Similarly, many low fecundity lines have originated with individuals which were themselves exceedingly high layers. Indeed one of the highest winter layers which have ever appeared in the stock evidently belonged to a genotype of very low fecundity, since it has never been able to produce progeny of anything but the poorest laying capacity. The breeding history of this bird (D352) is indeed so interesting that it may be briefly discussed here. This bird in her pullet year laid 98 eggs between November 10 and March 1 and made a record for the year of over 200 eggs. She was mated and produced plenty of eggs during the hatching season, but they hatched very badly. Only one female worth putting in the house was obtained. This pullet (E356) made a winter record of only 39 eggs, just about the general flock average. E356 was not mated. Her mother (D352) was kept over and bred to another male the next year, in the hope that as a fowl she might produce more and better chickens than she had as a pullet. As a matter of fact she was again able to produce during the whole

¹³ Nilsson-Ehle, H., "Kreuzungsuntersuchungen an Hafer und Weizen," *Lunds Univ. Arsskr.*, N. F., Afd. 2, Bd. 5, Nr. 2, 1909, pp. 1-122.

breeding season only one pullet worth putting into the laying house. This pullet (F163) made a winter record of but 11 eggs. F163 was bred in 1910, but produced only one daughter worth saving. This daughter, G429, has made a winter record of 18 eggs. It would be hard to get clearer evidence than that afforded by this breeding history that D352 belonged to a low fecundity genotype, in spite of her individual high laying record.

THE EFFECT OF THE SELECTION OF FECUNDITY GENOTYPES

Let us now consider the bearing of the results so far set forth on the problem of selection. Taking first the question of the effect of selection for fecundity within a population it is plain that if different degrees of fecundity have a genotypic basis, as the facts above presented and a considerable mass of data of a similar kind, which owing to lack of space can not be given here would appear to indicate, then the results following selection will depend entirely upon the genotypic constitution of the population. If high fecundity genotypes are present they can be isolated by selection. If they are not present selection of high laying hens will not change the average production of the flock.

The aim of the selection experiments since 1907 has been to discover and propagate separately genotypes of high fecundity and genotypes of low fecundity, all the birds being taken from the same general flock. The results of this work are shown in the following table and in Fig. 5. This table is to be regarded as a continuation of that given on p. 327, *supra*, which shows the results of mass selection for high fecundity in the same stock.

EFFECT OF SELECTION FOR FECUNDITY WITHIN THE POPULATION

1907-08.	Mean winter production of general population	15.92
1908-09.	Mean winter production of all high fecundity lines	54.16
1908-09.	Mean winter production of all low fecundity lines	22.06
1909-10.	Mean winter production of all high fecundity lines	47.57
1909-10.	Mean winter production of all low fecundity lines	25.05
1910-11.	Mean winter production of all high fecundity lines	50.58
1910-11.	Mean winter production of all low fecundity lines	17.00

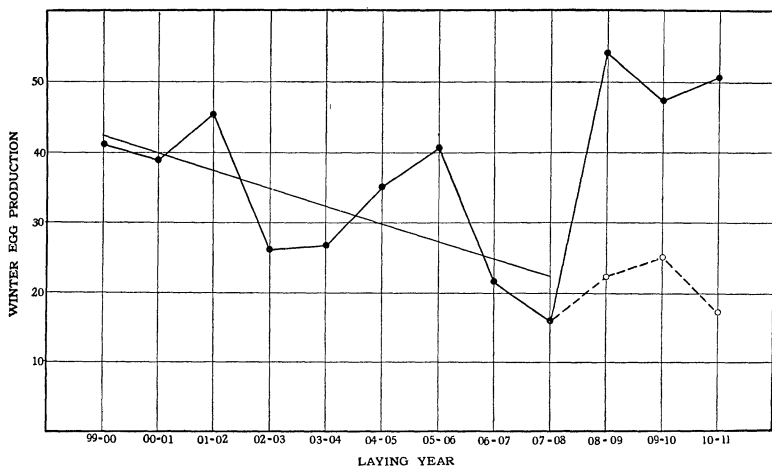


FIG. 5. Showing the effect of selecting high and low fecundity on a genotypic basis. The solid line denotes means of all "high lines"; the dotted line means of all "low lines." Up to 1907-08 the attempt had been to increase egg production by breeding merely from the highest layers, regardless of pedigrees. In 1907 and subsequent years the attempt has been to isolate genotypes of high and low fecundity which shall breed true, each to its own type.

The results indicate the effectiveness of this method of selection. It should be understood, of course, that only those pedigree lines are included in the high line averages which uniformly *in each generation* show high fecundity. A similar consideration applies to the low line averages.

Let us now consider briefly the question of the effectiveness of selection *within* the genotype. According to the "pure line" concept we should not expect selection of high or low individuals belonging to the same genotype to produce any effect, except in cases where segregation has occurred and the selected individuals are really gametically different, though having the same pedigree. An example of this sort has been given in the case of line D61D168 (cf. p. 331, *supra*). The ineffectiveness of selection within the line when something of this sort does not occur is illustrated by line D56D407. In the F_1 generation in this line there were four birds, of which three were good layers and one was a poor layer. Two of the good layers and the poor layer were bred.

Large families were reared in F_2 and F_3 . The average results in the three generations are given in the following table.

EFFECT OF SELECTION OF GOOD AND POOR WINTER LAYERS IN THE
SAME LINE, D56D407

Generation	F_1	F_2	F_3
Mean winter record of <i>good</i> layers and their progeny	76.0	46.7	35.57
Mean winter record of <i>poor</i> layers and their progeny	26.0	52.0	36.75 ¹⁴

It is evident that selection within the line here was quite without effect.

Another example of the same thing from line D31D447 may be given by way of further illustration. In this line there was in the F_1 generation a family of ten daughters. Of these some were very good and some were poor layers. All were bred. The mean results are shown in the next table.

EFFECT OF SELECTION OF GOOD AND POOR WINTER LAYERS IN THE
SAME LINE, D31D447

Generation	F_1	F_2	F_3
Mean winter record of <i>good</i> layers and their progeny	62.5	23.75	22.00
Mean winter record of <i>poor</i> layers and their progeny	32.0	28.75	14.75

Here again it is plain that selection within the line was without effect. Many more examples of the same sort might be given from the records did space permit. In general there is no evidence whatever that the selection of individuals of different laying records, but belonging to the same fecundity genotype, produces any definite or permanent effect whatever.

DISCUSSION AND CONCLUSIONS

Taking into consideration all the facts which have come out of this study, one is led to the following view as to the composition of a flock of fowls in respect to fecundity. In the average flock we may presume that there will probably be represented a number of fecundity

¹⁴ If one family of four birds, which ought not in fairness to be included here because they were extremely inbred (brother-sister mating) in connection with another experiment, is excluded this average becomes 49.0.

genotypes, some high, some low, and some intermediate or mediocre. In an ordinary flock these genotypes will be greatly mixed and intermingled. Further, the facts in hand indicate that the range of variation in fecundity *within* the genotype is relatively very large, nearly as great, in fact, as in the general population. Thus while fecundity genotype *means* may be and usually are perfectly distinct, there is much overlapping of individuals in the different lines. In consequence it results that the egg record of an individual bird is of almost no value in helping to tell in advance of the breeding test to what fecundity genotype it belongs. Essentially this same fact has been brought out in all of the work which has been done with pure lines. The only difference in the present case lies in the fact that the range and degree of variation within the line appears to be relatively greater in the case of fecundity than in the case of most characters hitherto studied, as, for example, size relations in beans or *Paramecium*.

The most serious difficulty which confronts one in the attempt to analyze the inheritance of a character like fecundity lies in the almost inextricable mingling of genotypes in the great majority of individuals. This, of course, is a direct consequence of the manner of reproduction. The germ plasm of two separate individuals must unite to form a new individual. By prolonging incestuous mating one may in theory come indefinitely close to reproductive purity, but in practise even this is extremely difficult, if not impossible of accomplishment on any large scale or through any long period of time. The fact simply is that a "pure line" in the strict sense of Johannsen¹⁵ can not by definition exist in an organism reproducing as the domestic fowl does. This, however, by no means indicates that the inheritance of fecundity does not rest on a genotype basis, or, in other words, that

¹⁵ Johannsen's definition is as follows: "Mit einer reinen Linie bezeichne ich Individuen, welche von einem einzelnen selbstbefruchtenden Individuum abstammen." ("Ueber Erbllichkeit in Populationen und reinen Linien," p. 9.)

fowls do not carry definite genes for definite degrees of fecundity.

We touch here upon an important point; namely, the relation of the mode of reproduction to the mode of inheritance. As one reflects upon the matter it becomes clear that it is only in the sense of a *reproductive* line that we can not, by definition, have pure lines in organisms where the sexes are separate. It is perfectly possible to have a line of such organisms in which all the individuals are *gametically* pure with reference to any particular character. For example, it is the simplest of matters to establish a line of horses pure in respect to chestnut coat color. Any individual in such a line mated to any other will never produce anything but chestnut offspring. So similarly with any other character, it is only necessary to obtain homozygous individuals in respect to any character in order to form a gametically pure strain with reference to that character.

It must further be kept clearly in mind that a reproductive "pure line" (in the sense of Johannsen's definition) may be made up of individuals *not* gametically pure (*i. e.*, homozygous). Thus suppose one crosses a yellow and a green pea and then takes an F_2 heterozygote individual seed which originated from a self-fertilized F_1 individual as the "single, self-fertilized individual" with which to start a line. The individual which starts such a line arose by self-fertilization and is selfed to produce progeny and would thus fulfil every requirement of a *reproductive* "pure line" as defined by Johannsen. Yet it would produce both yellow and green offspring. On the other hand, as already pointed out, a line which is not, and from the nature of its mode of reproduction never can be, reproductively "pure" may be gametically so (*i. e.*, have none but homozygous individuals with respect to any character).

We then see that the fact that in fowls the sexes are separate and we therefore can not have reproductive "pure lines" gives, *per se*, no reason to suppose that fe-

cundity is not inherited on a genotypic basis. We have to consider the problem of genetic or gametic purity. Do we have homozygote lines in such cases as those discussed in this paper? It plainly is the fact that one can get lines of birds which, broadly speaking, will breed true (perhaps throwing occasionally a few individuals not true to the type of the line) to definite degrees of fecundity. The same thing is true of milk production in dairy cattle, speed in race horses, etc. What are these lines gametically? Theoretically the formation of gametically pure (homozygote) lines with respect to definite degrees of fecundity is simple. Practically it is exceedingly difficult to do this, owing to the fact that (*a*) the character studied is not expressed in the male, and (*b*) it is subject to a wide fluctuating variability caused by environmental conditions. The question as to the gametic constitution of the fecundity lines here discussed obviously can not be answered finally now. It is a matter for much further research. One may, however, form a general conception of the probable gametic constitution of such lines, which has much evidence in its support. The essential points in such a conception are:

1. Probably no line yet obtained is absolutely pure gametically in respect to fecundity. It represents a mixture of a greater or less number of fecundity genes.

2. Lines which breed reasonably true to a definite degree of fecundity may in most cases be taken to be made up of individuals bearing a preponderant number of genes of the particular degree of fecundity to which the line breeds true, so that in gametogenesis a great majority of the gametes formed carry only these genes. They also carry some genes of higher, or lower fecundity, or both kinds. When individuals of a definite (*e. g.*, "high") line thus constituted are bred together the majority of the offspring will, purely as a matter of chance, be produced by the union of two high fecundity gametes. It is quite possible that with families of the size obtained with poultry nearly or quite every individual produced

in the line for several successive generations may be of this kind. In the long run, however, it is to be expected that a small number of "off" individuals will appear in the line. These originate by the chance union of two low fecundity genes, or by the union of a "high" gene with a "low" gene of great potency (as in the case of D31, cf. p. 335).

3. The degree to which such a line will breed true will depend upon the proportion of genes of one type (or of very similar types) present. The higher such proportion the less frequently will the "off" individual segregate out. The practical goal to be worked towards is, of course, to obtain several lines not closely related, but all made up only of individuals homozygous with respect to either high or low or any other definite degree of fecundity.

Whether a given degree of fecundity is to be regarded as a single unit character, in the Mendelian sense, or, on the other hand, as a complex dependent upon a particular combination of separately segregable unit characters, can not yet be determined. Every one must recognize the fundamental importance of the investigations of Nilsson-Ehle, Baur and East, which have shown that many characters which at first glance do not appear to conform to any determinate law of inheritance are really complexes, formed by the combination of a number of unit characters, each of which segregates and otherwise behaves in a perfectly regular and lawful manner. There are some facts which indicate that high fecundity is a character of this kind, but it will require prolonged analysis to decide this, because of the numerous practical difficulties which attend the study of fecundity.

A great help in this analysis, as well as a contributory line of evidence of much weight in supporting the general conception of the manner of inheritance of fecundity set forth above, is derived from the study of crosses between breeds of poultry in which high and low degrees of fecundity are definite breed characters. Studies of

this sort carried out at the Maine station indicate that the relatively high fecundity characteristic of the Barred Rock breed is inherited as a sex-limited character. In this respect it behaves like a simple unit character, but this does not necessarily prove that it is not a complex. More data are needed to settle this point. Of much significance is the fact that, whether simple or complex, fecundity is shown by these experiments in cross breeding to be a character resting on a definite gametic basis.

In conclusion, I think it may fairly be said that the investigations here reported show in the first place that different degrees of fecundity *are* inherited in the domestic fowl, and in the second place, that in all respects wherein it has been possible, considering the inherent difficulties of the material and the character dealt with, to make the test, the method of this inheritance is in entire accord with Johannsen's concept of genotypes.